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What individual life histories can (and cannot) tell about population dynamics

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Abstract

We present an overview of a long-term research programme that is aimed at revealing the relations between individual feeding, growth, reproduction and mortality in *Daphnia pulex* and the state and dynamics of the population. We analyse a physiologically structured population model, in which individual performance is described using an energy budget model that incorporates a food dependence. The model predictions are shown to be at odds with experimental observations on populations of *Daphnia*. We argue that these discrepancies are primarily due to insufficient knowledge about the precise size-scaling of the food ingestion rate, which plays a central role in the competitive interaction among individuals. To a lesser extent, the discrepancies arise because details about the energy budget of individual *Daphnia* are not sufficiently known for the food conditions prevailing in population experiments.

Introduction

Species of the genus *Daphnia* have been used extensively to study the behaviour and life history of individuals, the consequences of these individual-level processes for the dynamics of the population, and the significance of the individual behaviour on an evolutionary time scale. We have studied the interaction between *Daphnia* and its food source, consisting of an assemblage of algal species, with the aim to unravel the relations between population dynamical observations and individual life history traits (Nisbet et al., 1989; De Roos et al., 1990; Gurney et al., 1996; McCauley et al., 1996). An understanding of these relations is not only interesting in its own right, but is also important for resolving evolutionary questions. Mylius & Diekmann (1995) have clearly shown that to judge the adaptive value of, for example, diel vertical migration (Ringelberg, 1991; Lampert, 1993) or predator-induced life history shifts in *Daphnia* (Reede & Ringelberg, 1995), measurements of population growth rates or expected life-time reproductive success are most likely not conclusive. Instead, the density dependent processes regulating a population determine to a large extent whether or not an individual trait is evolutionary advantageous (Mylius & Diekmann, 1995). Whether or not specific types of individual behaviour constitute an adaptive strategy can therefore only be judged against the background of the full dynamics of both the population and the biotic and abiotic environment with which it interacts.

To link processes at the individual and the population level, the use of mathematical models seems almost inevitable. There is ample experimental evidence that the growth and development of individual *Daphnia* have considerable influence on the state and dynamics of the population (McCauley & Murdoch, 1987). If such influences have to be accounted for in a population dynamic model, a classical description in terms of ordinary differential equations that only keep track of the total population size or biomass will not suffice. Instead, *physiologically structured population models* (Metz & Diekmann, 1986; Nisbet et al., 1989; De Roos, 1997) have to be used. Structured and, more generally, individual-based population models (DeAngelis & Gross, 1992; Tuljapurkar & Caswell, 1997)

describe the dynamics of a population entirely on the basis of the behaviour and life history of its individuals by means of some form of bookkeeping. To formulate a structured population model, one first has to construct a model of individual performance, that is, of individual growth, reproduction, development and mortality as a function of the state of the individual itself and the state of its environment. The equations governing the population state and changes therein can subsequently be derived without making any additional assumptions. In this way, structured models describe the population dynamics explicitly as the resultant of the performance of its individuals.

Individual-based and structured population models have recently become very popular and their use is likely to increase only. Many studies have used individual-based models to generate possible explanations for population observations in terms of individual behavioural mechanisms (see examples in DeAngelis & Gross, 1992, and Tuljapurkar & Caswell, 1997). However, only few have generated testable hypotheses and have rigorously confronted them with experimental data. For reliable predictions at the population level, we have argued that the mathematical model of individual performance, which forms the core of any individual-based model, has to be tested against independent experimental data (Murdoch et al., 1992). Subsequent to this modeling and validation stage at the individual level, the population can be studied as a collection of (model) individuals that possibly interact with each other and their environment. The resulting predictions should be tested against independent observations on populations.

Our ultimate research aim is to generate testable hypotheses about the dynamics of predator-prey systems. Because of the wealth of empirical data on both the individual and the population level we have adopted *Daphnia* and its algal food source as an example system. One of the key questions we have addressed is whether it is possible to generate predictions about the state and dynamics of the population entirely based on information about individual life histories and their dependence on environmental (mainly food) conditions. To this end we have combined experimental studies, both in laboratory and semi-natural microcosm systems, and modeling exercises with different levels of complexity (Nisbet et al., 1989; De Roos et al., 1990; McCauley et al., 1990a,b, 1996; Gurney et al., 1990; Nisbet et al., 1996). As one of the approaches, we constructed a stage-structured model that only distinguishes between juveniles and adults. Central to this model is the empirical relation between juvenile stage duration and ambient food levels (Nisbet et al., 1989; McCauley et al., 1990a), which phenomenologically reflects the aspects of the individual energy budget that are important for juvenile development and consequently for population dynamics. This model successfully predicted the characteristics of cyclic dynamics in *Daphnia* that are commonly observed under a wide range of conditions (McCauley & Murdoch, 1987; Nisbet et al., 1989). In addition, the model was shown to explain the outcome of competition experiments between *Daphnia* and *Bosmina* under different feeding regimes (McCauley et al., 1996).

In this paper we present some results on one of the more complicated structured population models, which is based on energy budget considerations of an individual *Daphnia*. Individual ingestion, assimilation and subsequent use of energy for growth, maintenance and reproduction are food- and size-dependent following a tested model of individual performance (Gurney et al., 1990; McCauley et al., 1990b). Pure exploitative competition for food is assumed to be the only interaction among individuals. The resulting population model is shown to yield predictions that are at odds with observations on a *Daphnia pulex* population in the laboratory. We will argue that insufficient information about the size-dependency of the interactions among individual *Daphnia* in a population is the main source of the discrepancies between the model predictions and the experimental observations. We will discuss the implications of our results for the construction of individual-based population models in general and the collection of experimental data that are required for their formulation.

A model of individual feeding, growth and reproduction

The target data set that we use to test our model predictions is derived from controlled laboratory experiments with populations of one specific clone of *Daphnia pulex*. Three different populations of *D. pulex* were grown in 275 ml containers and transferred three times a week (on Monday, Wednesday and Friday) to new containers with fresh medium. The food concentration of the fresh medium was 6×10^7 cells of *Chlamydomonas rheinhardii* per liter, which was measured at the end of the experiments to be equivalent with 3.5 $\mathrm{mgC} \cdot \mathrm{l}^{-1}$ (58 pgC per cell). The entire population was counted and the size of all individual *Daphnia* was determined

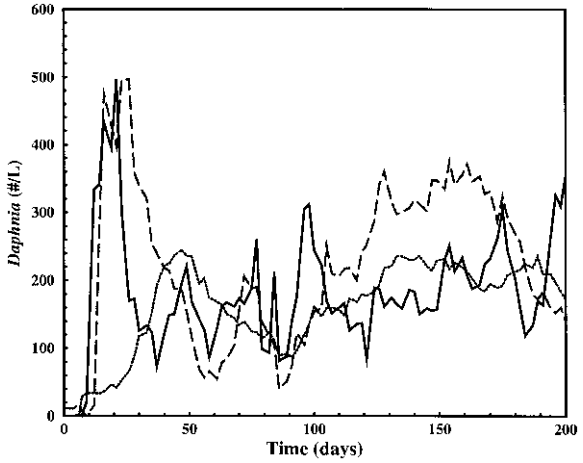

Figure 1. Average dynamics of three laboratory populations of *Daphnia pulex* living in a 275 mL container with *Chlamydomonas rheinhardii* as its food source. Food concentration of fresh algal medium: 3.5 mgC $\cdot$ l^{-1}. The populations were transferred to new containers on Monday, Wednesday, and Friday. Solid line: individuals with $L < 1.0$ mm; Dashed line: individuals with 1.0 mm $< L <$ 1.6 mm; Dotted line: individuals with $L > 1.6$ mm. Data as reported in Nisbet et al. (1996).

at each transfer to new medium. Hence, the entire state of the three populations was assessed with minimal sampling error. The average dynamics of the *Daphnia* populations, subdivided into three different size classes, is shown in Figure 1. Details about these experiments can be found in Nisbet et al. (1996).

Because of the controlled experimental conditions we assume that exploitative competition for food is the only relevant interaction among the individual *Daphnia* constituting a population. Changing food levels influence growth, development and reproduction in *Daphnia* to a large extent. To model individual performance, it is convenient to use energy as the common unit and hence model the entire process of energy acquisition by feeding and energy allocation to somatic growth, basal metabolism and reproductive output. Such *dynamic energy budget* models (Kooijman, 1993) often constitute the core of physiologically structured population models, in which body size is the main individual trait determining performance.

In previous studies, we developed such a model for the individual energy acquisition and spending for *Daphnia pulex* (Gurney et al., 1990; McCauley et al., 1990b). The model for the feeding, growth, development and reproduction (Gurney et al., 1990; McCauley et al., 1990b) was parameterised for an individual *D. pulex* feeding in isolation on *Chlamydomonas rheinhardii*. It was successfully used to predict the experimental observations on the growth and reproduction of *D. pulex* from ten distinct life-history experiments using a variety of experimental protocols and food concentrations. The experimental observations used to test the model were independent from the experimental data employed to develop the model (Gurney et al., 1990). All data were extracted from the literature and were collected by a variety of different experimentalists (Richman, 1958; Paloheimo et al., 1982; Taylor, 1985; Lynch et al., 1986). Its success in predicting these experimental observations from a number of different sources, inspires trust in the validity of the developed energy budget model (Gurney et al., 1990). Note, however, that such tests with data from individuals raised in isolation can only verify the part of the model dealing with the use of assimilated energy. Energy acquisition, and hence the interaction among individuals, is described on the basis of a relationship between maximum ingestion rate and individual length, based on observations by Lynch et al. (1986).

In the model, individual *Daphnia* are characterised by their weight W, their length L, the amount of energy E allocated to and available for reproduction of the next clutch of eggs, and the number of eggs presently carried in the brood pouch N_e. Individual weight W is measured in terms of body carbon and hence comprises both structural body mass, like muscles, and energy reserves, such as fat droplets. Individuals are assumed to moult every $T_m = 2.0$ days, on which occasion they shed their carapace, release their eggs and have the possibility to grow in length and to deposit new eggs in the brood pouch. Individual length L and the number of eggs in the brood pouch can therefore only change whenever a moult takes place, while the individual weight W and the energy allocated and available for reproduction changes continuously over time.

Figure 2 shows a schematic representation of the major energy pathways, incorporated in the individual-level model. The main assumptions of the model regarding the energy flows along these pathways can be summarized as follows:

(1) Ingestion of food is determined by the maximum food ingestion rate which depends on individual length and by the current food density following a Holling type II functional response. The maximum ingestion rate is proportional to $L^{2.4}$ (McCauley et al., 1990b), based on the data from Lynch et al. (1986).

(2) Assimilation efficiency of ingested food is assumed constant.

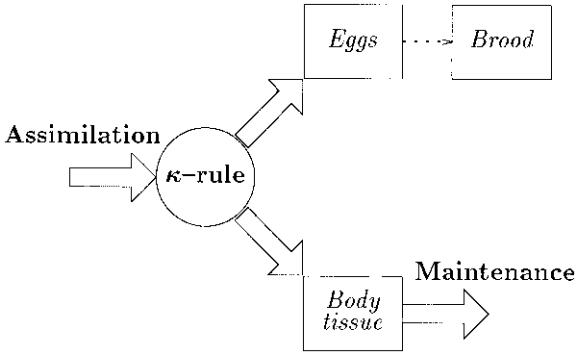

Figure 2. The energy channeling scheme of the *Daphnia* model (after Gurney et al., 1990).

(3) Maintenance requirements depend on the individual weight following an allometric relation and always take precedence over growth in weight.

(4) The *proportion* of assimilated energy channeled to reproduction is 0 as long as the individual length is smaller than some minimum value $L_m = 0.9$ mm, and thereafter increases nonlinearly with increasing length and increasing food concentration.

(5) Whenever an individual moults, it releases the eggs and deposits a new clutch of eggs in the brood pouch, provided it has allocated sufficient energy to produce at least one egg.

(6) The amount of energy required to produce one egg depends on the ratio of the total amount of energy committed to reproduction during the preceding intermoult period and the amount of energy that the individual would have allocated to reproduction when feeding at its maximum feeding rate.

(7) An individual that has gained sufficient weight during an intermoult period will increase in length when shedding its carapace. The model assumes in this case that its new length right after moulting is completely determined by its current weight, following a constant relationship, referred to as the *weight-for-length* relation. The weight-for-length is interpreted as the 'characteristic' weight, pertaining to the individual's length. It is also adopted as an indicator of the individual condition. Whenever prolonged periods of food shortage cause the actual weight to drop below the weight-for-length, the individual is considered starving. On the other hand, an individual with an actual weight above its weight-for-length can increase its length when moulting. It then grows in length such that weight and weight-for-length are equal. Starving individuals do not change in length when moulting.

(8) The allocation rule changes during starvation, that is when the actual weight drops below the individual's weight-for-length, or when the amount of energy assimilated is less than the maintenance requirements, in which case allocation of energy to reproduction stops completely. In such circumstances, the maintenance requirements are covered first, while the remaining energy ingested is used to restore the weight-for-length relation.

(9) In this paper we assume that individual *Daphnia* experience a constant, background mortality. The only other source of mortality is starvation, which induces immediate death as soon as the actual individual weight drops below 50% of its weight-for-length. A background mortality rate of 0.06 per day was used throughout the simulations. This roughly equals the observed, average daily mortality of individuals of this clone when raised in isolation under low food conditions (McCauley et al., 1990a).

The description above gives only a short outline of the energy budget model that is used in the population model studied in the next section. For more details, see Gurney et al. (1990) and McCauley et al. (1990b).

The population model and its predictions

The energy budget model from the previous section forms the core of the individual-based or structured population model. The model is sufficiently complicated to prohibit any analytical investigation and we have therefore explored its dynamics only numerically. Using the *Escalator Boxcar Train* technique (De Roos, 1988; De Roos et al., 1992), the population was represented as a collection of cohorts, each cohort consisting of the offspring produced by one female in a single brood. Neonate individuals are assumed to be identical. The individual-level model deterministically describes their growth, development, and reproduction, dependent only on their own state and the current food density. Individuals within a cohort will hence moult and possibly reproduce at the same time. The population dynamics thus consists of pulses of reproduction by single cohorts (whenever the individuals within it moult) with deterministic growth, feeding and development of all individuals in between these reproduction pulses.

To test model predictions against experimental observations the population dynamics was simulated for the exact feeding regime of the population experiments. Hence, the model was used to predict the

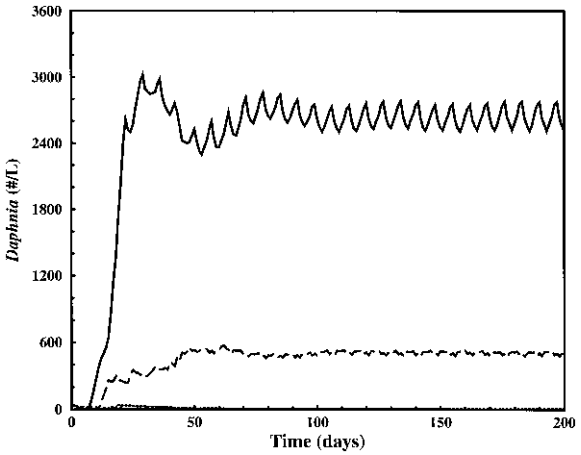

Figure 3. Population dynamics of *Daphnia pulex* feeding on *Chlamydomonas rheinhardii*, as predicted by the structured population model. The model incorporates the exact experimental protocol of the population experiments, shown in Figure 1. All individuals are assumed to experience the same constant, background mortality of 0.06 per day. Solid line: individuals with $L < 1.0$ mm; Dashed line: individuals with 1.0 mm $< L <$ 1.6 mm; Dotted line: individuals with $L > 1.6$ mm.

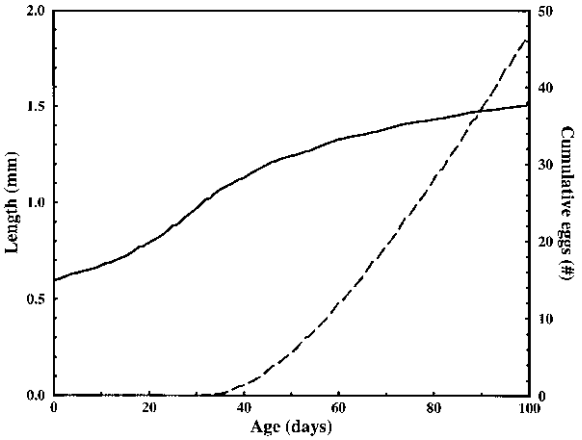

Figure 4. Length-age relation (solid line) and the relation between the cumulative number of produced eggs and age (dashed line) as predicted by the structured population model.

dynamics of a *Daphnia* population living in a 275 ml vessel with non-growing food, the density of which was reset to a value of 3.5 mgC $\cdot$ l^{-1} on Monday, Wednesday and Friday. In between, the food density only decreased due to feeding by *Daphnia*. The default values for the parameters of the energy budget model (see Gurney et al., 1990) were used. Figure 3 shows the predicted dynamics for the three different size classes (small, intermediate and large) that were also distinguished in the population experiments (cf. Figure 1). The population reaches a steady state after a transient phase of approximately 200 days. The total size of the model population ends up around 3800 *Daphnia*.

The predictions of the population model differ substantially from the experimental observations. Although the total biomass predicted by the model was reasonably close to its experimentally observed value (5.5 versus 4.1 mgC $\cdot$ l^{-1}, respectively), the model obviously predicts the presence of far too many individuals (3800 versus 700 *Daphnia* $\cdot$ l^{-1}). Moreover, the majority of these individuals are small: individuals larger than 1.6 mm are totally absent, while they constitute roughly a third of the experimental population. Individual growth in the simulated population is thus significantly lower than in the experimental population. Figure 4 shows the relation between the length of an individual *Daphnia*, the cumulative number of eggs it produced, and its age, that are ultimately observed in the model population. The length-age relation has a sigmoidal form where individuals reach characteristic adult sizes around 1.5 mm only after sixty or more days. The relation between the cumulative number of eggs and age is characterised by a long juvenile period of around forty days and a rapid egg production up to almost one egg per day after maturation. These aspects are in sharp contrast with general observations on individual *Daphnia pulex*, which exhibit a rapid juvenile growth, a juvenile stage duration that even under the lowest food conditions does not exceed twenty days (McCauley et al., 1990a) and characteristic sizes at first reproduction around 1.4 mm.

The most striking differences between the model predictions and the experimental data hence are:

(1) The overestimation of the total population size with far too many individuals of sizes below 1.0 mm and no individuals with size above 1.6 mm,

(2) The sigmoidal form of the length-age relation, and

(3) The absence of any egg production up to ages around forty days.

Since the model population ultimately approaches a steady state, every newborn individual on average replaces itself. With a juvenile period lasting forty days, only 9% of all neonate *Daphnia* reach adulthood. Obviously, the rate of reproduction after maturation is sufficiently large to make up for this long juvenile delay with its low survival. The population is thus clearly 'delay-regulated' instead of 'fecundity–regulated' (Gurney et al., 1996). The *Daphnia* population and its food source constitute a strongly regu-

lated feed-back loop. The feed-back control ensures that the juvenile period has to be extended, because the average, total reproductive output as an adult would otherwise greatly exceed a single offspring. Hence, maturation is postponed by slowing down juvenile growth considerably, especially for the youngest and smallest individuals. As a consequence of the sigmoidal growth curve and the delayed onset of reproduction, the length-distribution of the population is strongly skewed towards smaller sizes, which is clearly at odds with the observed population composition shown in Figure 1.

Possible explanations for the discrepancies between the model predictions and the population observations roughly fall into three different categories that will be discussed in the following sections.

Survival

In the current model it is assumed that all individuals experience the same, constant background mortality rate and that individuals die instantaneously when their weight falls below 50% of their weight-for-length. In reality, death rates will vary more gradually with the current food condition, individual size and the starvation condition of the individuals. To assess whether the assumption of a constant background mortality is responsible for the discrepancies we also studied a version of the population model, incorporating a complicated food- and size-dependent death rate for all individuals. This sub-model of individual mortality accurately captured observed survival in cohorts of individuals from the same clone of *Daphnia* under a variety of food conditions (McCauley et al., 1990a). The results of the population model did not exhibit qualitative changes when the constant background mortality was replaced by a food- and size-dependent death rate. This is primarily due to the fact that both the food- and size-dependent mortality model and the random background mortality rate of 0.06 per day predict the same average lifetime of 16–17 days for an individual *Daphnia* living under low food conditions. Replacing the random mortality with a food- and size-dependent mortality hence did not affect the average daily mortality rate, but only its variation with size and food density.

Energy usage

Although the model of individual energetics was developed on the basis of a large set of literature data and tested successfully against an entirely independent set of experimental observations on individuals, it is possible that the energy budget model does not accurately describe the use of energy by the individuals in the experimental population. All data used in developing and testing the energy budget model were collected under experimental conditions that imposed higher levels of food availability on the individuals than experienced in the experimental populations. The daily ration of food supply in the experimental population studies presented in Figure 1 equals approximately 0.02 mgC per individual per day. The food supply in the individual experiments on which the energy budget model is based was usually 5–10 times larger. Experimental data that have become available more recently (McCauley et al., 1990a) indeed indicate that individual growth, development and reproduction change qualitatively when the food concentrations experienced by the individuals are decreased. More specifically, individuals seem to spend a larger proportion of the assimilated energy on somatic growth and less than on reproduction such that even under low food levels individual sizes above 2.0 mm are frequently reached. This performance is not to be expected on the basis of the experimental data collected from individuals living under higher food levels. The energy budget model extrapolates consistently the individual performance under these higher food levels and hence naturally fails to capture the qualitative changes in individual performance that occur when food levels are decreased (McCauley et al., 1990a).

We have investigated a number of plausible changes in the individual energy channeling that are known to occur under low food conditions. In general such adaptations do not qualitatively change the three main differences between model predictions and experimental observations. For example, assimilation efficiency has been found to increase with a decreasing food concentration (Urabe & Watanabe, 1991). Varying the efficiency between 60% (the default value) and 90% had no effect on the very skewed size-distribution predicted by the population model, as opposed to the relatively even size-distribution observed in the experiments. Furthermore, the energy budget model used here predicts that the amount of energy required to produce a single egg increases with increasing food conditions. It is unclear whether this energy investment is directly related to the neonate size, but the latter has been shown to vary in a rather complicated manner with food conditions. Glazier (1992) showed for two different clones of *Daphnia magna* that neonate size

was either constant or decreased with increasing food conditions, depending on the clone and the volume of the experimental container. We verified that assuming a constant energy investment of 1.23 μgC per egg (Paloheimo et al., 1982), does not significantly alter the model predictions.

The relation between weight and length right after moulting for growing individuals (the 'weight-for-length' relation) that is used in the individual model as an indicator of condition, was based on observations by Paloheimo et al. (1982). Although in the individual model weight and length can still vary independently when food conditions fluctuate, the weight-for-length relation is independent of food conditions. In an independent set of experiments we have verified that this weight-for-length relation, as proposed by Paloheimo et al. (1982), not only holds for our clone of *D. pulex*, but also that this relation does not significantly change with feeding conditions (Noonburg et al., in press).

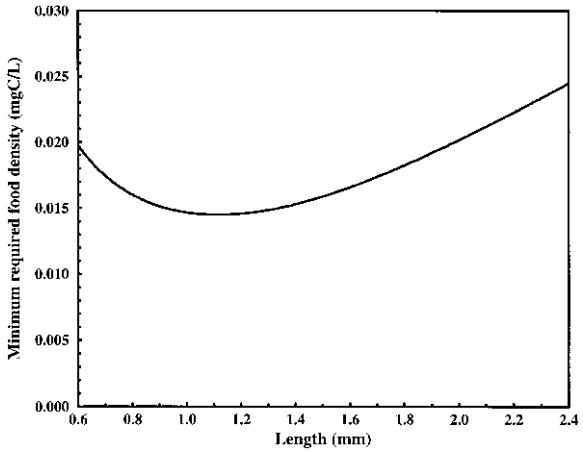

Figure 5. Minimum food density required to just cover basal metabolic energy expenditure for individual *Daphnia* of different sizes in the energy budget model proposed by Gurney et al. (1990). This minimum food level is derived by finding for each individual size separately the food density at which the (length-dependent) energy assimilation rate equals the (length-dependent) maintenance rate.

Energy acquisition

The model population is conceived to consist of individuals that only interact by pure exploitative competition and neglects direct interactions between the individuals, such as decreased growth rates due to crowding (Burns, 1995). The interactions between individuals are hence largely determined by the length-dependent feeding rate.

Elsewhere we have shown that an extended life table analysis of the experimental observations on individual growth, reproduction and survival reported by McCauley et al. (1990a) can correctly predict the size and composition of the experimental *Daphnia* populations shown in Figure 1 (De Roos et al., 1997). This suggests that the individual life history which is observed in experiments with individuals in isolation is representative for the life history of the individuals in the experimental populations. However, the occurrence of this individual life history in the experimental populations is not to be expected on the basis of the scaling relation between ingestion rate and individual length. This point is illustrated in Figure 5, which shows the minimum food level required to cover the basal metabolic costs for individuals of different sizes. This minimum food level is derived by finding for each individual size the food density at which the (length-dependent) energy assimilation rate equals the (length-dependent) maintenance rate. It can be interpreted as a measure of the individual competitiveness in the intraspecific competition for food. Clearly, individuals with length around 1.2 mm are most competitive and hence manage to secure a large proportion of the available resources. Neonate individuals, on the other hand, are rather inefficient. These observations relate to the slow neonate growth and the high reproductive output of individuals with sizes between 1.2 and 1.4 mm that are central to the discrepancies between the model predictions and the experimental observations.

The scaling of individual ingestion with length constitutes the major difference between the life table analysis presented by De Roos et al. (1997) and the population model presented here. Both analyses used the allometric relation between maintenance and weight, the weight-for-length relation and the same constant assimilation efficiency. The success of the life table analysis hence suggests that the ingestion-length relation is an important source of the discrepancies between model predictions and observations. In the model population a more realistic life history with rapid juvenile growth and juvenile stage durations up to twenty days might only occur if juveniles are also more competitive than suggested by Figure 5. Scaling relations between ingestion rate and length should have an allometric exponent probably less than 1.0 to achieve this increase in juvenile competitiveness. The exponent of the scaling relation implemented in the current model is approximately 2.4. This value is derived from a large number of experiments that all aimed at establishing the maximum individual feeding rate as a

function of individual size during short-term exposure of previously starved *Daphnia* to radioactively labeled algal suspensions. Most probably, such feeding experiments of short duration do not accurately reflect the food gathering capacity of individual *Daphnia* in the experimental populations on time scales that are much longer. Although crowding (Burns, 1995) might induce changes in food gathering capacity in a population context, it is important to note that the size-dependency of the ingestion rate is the crucial aspect. A constant reduction of the ingestion rate for all individual sizes due to crowding effects, would still lead to the same large deviations between the model and the observations. The rapidly changing food conditions that are characteristic for a population in batch culture could also induce changes in the scaling of ingestion rate and length, as measurements of individual ingestion are usually carried out in more constant food conditions. Population experiments carried out by Crabtree (1975) in flow-through systems exhibit, however, a similar population composition as reported here (Figure 1) with a roughly equal proportion of small, intermediate and large individuals. The population model predicts also for such flow-through food conditions a size distribution that is very much skewed to smaller individuals thereby discounting rapid fluctuations in food as a possible explanation for the observed discrepancies.

Discussion

In this paper we have presented a very limited overview of the results that we obtained when modeling a population of *Daphnia pulex* entirely on the basis of assumptions about the acquisition and spending of energy by individual organisms. A more detailed account of the model results would, however, go beyond the scope of the current paper. Our main aim in relating these findings is to point out two inherent difficulties in our attempts to unravel causal relations between individual life history and phenomena at the population level. These difficulties have important implications for future research on the population dynamics of *Daphnia* and, more generally, for the construction of structured or individual-based population models that are developed to predict population dynamics entirely on the basis of individual performance.

First of all, the model of individual performance that forms the core of the population model should preferably be developed on the basis of experimental data that are collected under conditions which resemble the conditions occurring in field populations. We have followed the more often used route of constructing a model of individual energetics on the basis of published literature data. Even though we validated the individual-level model (Gurney et al., 1990), we have to conclude that the experimental protocol used to collect the data on individual performance prohibit their extrapolation to food conditions that occur in experimental populations. The differences in the food conditions used in laboratory experiments with isolated individuals and those occurring in population studies with *Daphnia* have inspired us to carry out life history experiments under very low food conditions (McCauley et al., 1990a). These experiments indicate qualitative changes in individual performance with a decrease in food conditions. Although such qualitative changes may not be surprising, their occurrence has implications for the construction of structured population models. To generate realistic population predictions using such population models it is required that experimental and theoretical developments are tuned to each other. In the most optimal scenario, the development of a model of individual energetics and the collection of experimental data to derive functional relationships and parameter values for the model should be an iterative process with theoreticians and experimentalists working closely together. It is this interaction that in our opinion will allow us to ultimately reach our goal of predicting population dynamical phenomena entirely on the basis of individual biology.

The second important conclusion resulting from our model study is that interactions among individuals within a population are, even for species like *Daphnia*, not sufficiently understood and deserve far more attention. Which factors exactly play a role in this intraspecific competition for food resources and how individuals manage to secure sufficient resources to follow realistic growth and reproductive schedules in the face of this competition is yet unclear. As argued in the previous section, the model predictions turn out to be very sensitive to rather subtle changes in the scaling of ingestion rate with individual length. Such details of the interactions among individuals might hence also crucially influence the state of the experimental population. We have the impression that experiments are currently biased towards collecting information about life histories of individuals in isolation, even though there is unequivocal evidence that the interactions among individuals and the density dependence resulting from them are crucial for an understanding of

the population dynamics on an ecological time scale and the evolution of life histories on longer time scales.

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